THE ORIGIN OF THE CROCODILOID TARSI AND THE INTERRELATIONSHIPS OF THECODONTIAN ARCHOSAURS

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ABSTRACT. The tarsus of the proterosuchian *Chasmatosaurus* represents the primitive archosaur tarsus. This kind of tarsus is also present in rhynchosaurids, trilophosaurids, prolacertids, and *Protorosaurus,* and suggests that these reptiles are members of a single radiation. Two distinct kinds of crocodiloid tarsi are present in thecodonts, a crocodile-normal tarsus and a crocodile-reversed tarsus. The crocodile-reversed tarsus could have originated from the crocodile-normal tarsus, but the reverse relationship is not plausible. *Gracilisuchus,* the only "ornithosuchid" with a crocodile-normal tarsus, shows features of the skull that are not consistent with its placement in the Ornithosuchidae. *Euparkeria,* on the basis of both cranial and postcranial characters, is a plausible ornithosuchid ancestor but could not be ancestral to a pseudosuchian with a crocodile-normal tarsus. The tarsus of *Erythosuchus* neither contradicts nor supports a relationship between *Erythrosuchus* and rauisuchids.

INTRODUCTION

In recent years, it has been recognized that a number of structurally distinct kinds of tarsi are present in archosaurs, and an understanding of the evolution of this structural complex is necessary for an understanding of the interrelationships of the group. In the tarsus of crocodiles and typical pseudosuchians, the ankle joint passes between the astragalus and calcaneum, the astragalus being locked to the tibia and the calcaneum integrated with the pes. In dinosaurs, the ankle joint passes distal to the astragalus and calcaneum. Krebs (1963, 1973) argued that this

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difference precludes derivation of dinosaurs from any known pseudosuchian. Recently, two additional kinds of tarsi have been recognized in thecodonts. Proterosuchian thecodonts of the family Proterosuchidae have a distinct tarsus that is in many ways primitive (Cruickshank, 1972; Carroll, 1976). Bonaparte (1971) recognized that two distinct kinds of crocodilelike tarsi are present in pseudosuchians, one like that of crocodiles in which the astragalus has a peg that fits in a socket on the calcaneum, and one seen in advanced ornithosuchids in which the calcaneum has a process that fits in a socket on the astragalus. Chatterjee (1978) termed these the crocodile-normal and crocodile-reversed tarsus respectively. Also, two pseudoschians with mesotarsal ankle joints have been described (Romer, 1971). One of these, *Lagerpeton,* has a fully developed mesotarsal joint. The second, *Lagosuchus,* retains a posteriorly directed calcaneal tuber and a complex articulation between the astragalus and calcaneum (Bonaparte, 1975a).

The evolution of these tarsal patterns was recently discussed by Cruickshank (1979). Cruickshank showed that the proterosuchian tarsus is an excellent structural ancestor to the crocodile-normal tarsus and argued that the two kinds of crocodile tarsi can be used to separate pseudosuchians into two groups. Based on this, Cruickshank suggested that *Gracilisuchus,* which has a crocodile-normal tarsus, be removed from the Ornithosuchidae, all other members of which have a crocodile-reversed tarsus. However, the origin of the crocodile-reversed tarsus remains unknown. If the crocodile-normal tarsus was ancestral to the crocodile-reversed tarsus, then a crocodile-normal tarsus could have been present in primitive ornithosuchids, and the presence of a crocodile-normal tarsus would not bar *Gracilisuchus* from the Ornithosuchidae. Thus, in order to use the structure of the tarsus as a basis for interpreting the interrelationships of archosaurs, it is necessary to obtain a more precise understanding of both the origin of the crocodile-reversed tarsus and the phylogenetic position of *Gracilisuchus.*

THE CROCODILE-NORMAL TARSUS

In extant crocodiles, five elements are present in the tarsus: the astragalus, the calcaneum, and the second to fourth distal tarsals.

The astragalus (Fig. 1C-D) supports the tibia and contacts the fibula by articular surfaces that almost completely cover the proximal surface of the bone. Anteriorly, the astragalus has a strongly covex surface that articulates with the proximal end of the first two metatarsals and the medial surface of the second and third distal tarsals. Above this, the anterior face of the astragalus is formed by a concave area covered by finished bone. Laterally, a distinctive articular surface for the calcaneum is present. This is divisible into two separate areas. The ventral area has the shape of a portion of a
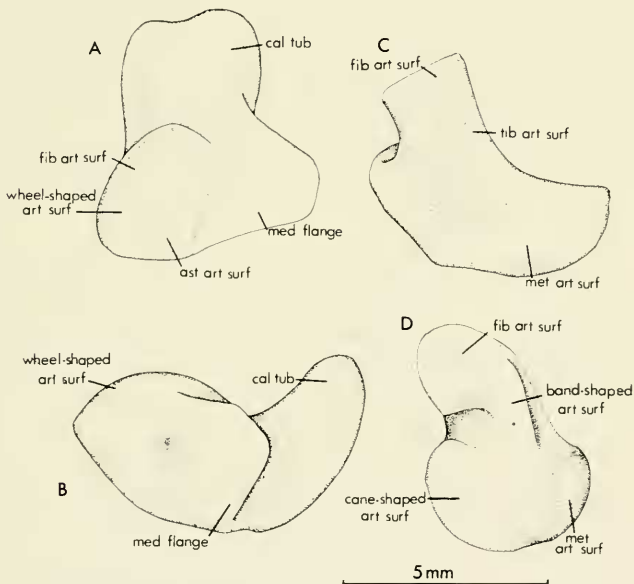

Figure 1.   The right astragalus and calcaneum of *Caiman sclerops.* A) calcaneum in proximal view; B) calcaneum in medial view; C) astragalus in dorsal view; D) astragalus in medial view.

Abbreviations: band-shaped art surf, band-shaped articular surface; cal tub, calcaneal tuber; cone-shaped art surf, cone-shaped articular surface; fib art surf, fibular articular surface; med flange, medial flange; met art surf, metatarsal articular surface; tib art surf, tibial articular surface; wheel-shaped art surf, wheel-shaped articular surface; ast art surf, astragalar articular surface.

cone, its apex forming the tip of the laterally directed peg. Dorsal to this, a notch in the lateral edge of the astragalus leads to a band-shaped articular surfce. These two areas meet along a ridge that terminates on the tip of the lateral peg.

The calcaneum (Fig. 1A-B) has three characteristic areas: a dorsal area that has the form of a portion of a wheel, a medially directed flange that underlies the astragalus, and a posteriorly directed tuber. The medial half of the wheel-shaped articular surface fits in the notch on the lateral edge of the astragalus and is overlapped by the astragalus. The lateral half supports the fibula. The fibular and astragalar surfaces are differentiated by a slight change in the curvature of the articular surface. The medially directed flange articulates behind the cone-shaped articular surface of the astra-galus. The calcaneal tuber extends across the full width of the bone. The distal end of the tuber is expanded and has a vertical groove in which lie tendons of the long pedal flexors. Anterodistally, the calcaneum as a flat articular surface that abuts the fourth distal tarsal.

A crocodile-normal tarsus is present in the Rauisuchidae (Krebs, 1965, 1973; Sill, 1974), the Aetosauridae (Sawin, 1947; Walker, 1961; Bonaparte, 1971; Sill, 1974), and *Gracilisuchus* Bonaparte, 1975b). A crocodile-normal calcaneum from the uppermost Lower or lowermost Middle Triassic was figured by Young (1964, Fig. 60) and attributed to *Wangisuchus.*

The astragalus in these pseudosuchians, where known, differs from that of crocodiles in having more extensive development of finished bone on its anterior face and in the proportions of the articular surfaces, the metatarsal articular surface being narrower mediolaterally in most genera, as in *Gracilisuchus* (Fig. 4B). The proportions of the calcaneum also show some variation, the calcaneal tuber of aetosaurs being considerably broader than in crocodiles and other pseudosuchians (Sawin, 1947). Despite this variation, the structure of the joint between the astragalus and calcaneum is like that of crocodiles.

THE TARSUS OF *CHASMATOSAURUS*

The tarsus of the early proterosuchid *Chasmatosaurus*[1] (Fig. 2) is primitive in the presence of a separate astragalus and centrale, and

the retention of a foramen between the astragalus and calcaneum. However, comparison with an eosuchian tarsus, such as that of a tangasaurid (Fig. 3), demonstrates that a number of derived features are present. The articular surface between the astragalus and calcaneum in eosuchians is flat and forms a straight line when the tarsus is seen in dorsal view. In *Chasmatosaurus*, the portion of the articular surface proximal to the perforating foramen is inclined relative to the distal portion, with the astragalus overlying the calcaneum. The articular surface between the astragalus and calcaneum is a complex concave-convex joint. The portion of the articular surface distal to the perforating foramen is a ball and socket joint, with the socket on the calcaneum. Proximal to the perforating foramen, a concave-convex joint is also present, but the concavity is on the astragalus. The proximal edge of the calcaneum is not preserved in *Chasmatosaurus vanhoepeni*, but in the
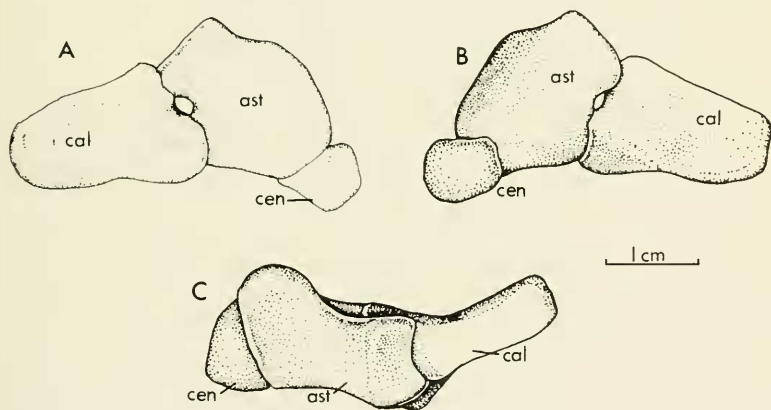

Figure 2. The tarsus of *Chasmatosaurus vanhoepeni*. Left calcaneum, astragalus, and centrale in A) ventral, B) dorsal, and C) proximal views. Drawing based on cast of NM C3016, Nasionale Museum, Bloemfontein.

Abbreviations: ast, astragalus; cal, calcaneum; cen, centrale.

[1]Following Charig and Sues (1976), *Proterosuchus* is considered a nomen dubium, and the remaining proterosuchid material from South Africa is referred to the genus *Chasmatosaurus*.
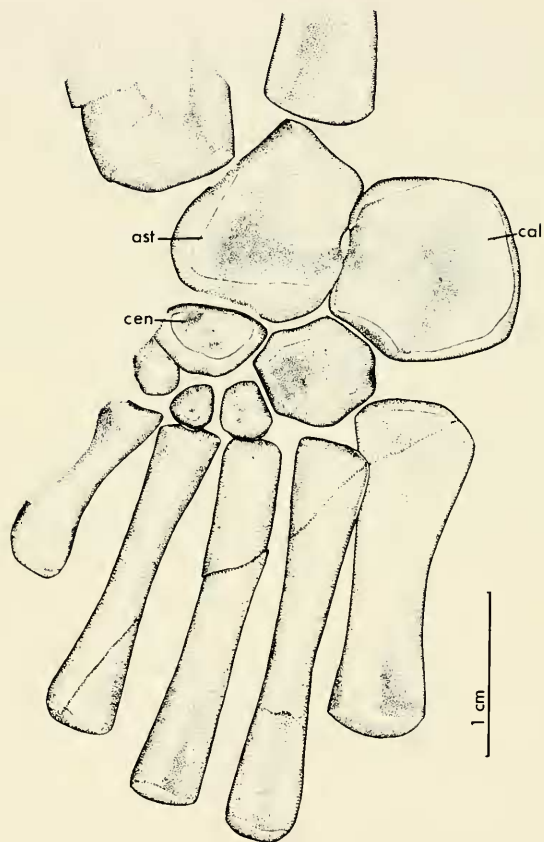
Figure 3.   The left tarsus of *Hovasaurus,* a tangasaurid eosuchian, in dorsal view.
Drawn from cast of MNHN 1925-5-61, National Museum of Natural History, Paris.

Abbreviations: ast, astragalus;   cal, calcaneum;   cen, centrale.

calcaneum of *Chasmatosaurus yuani* illustrated by Young (1936, Fig. 9D) the convexity of the calcaneal surface is seen to continue laterally to form a dorsoventrally convex fibular articular surface, as it does in the early rhynchosaur *Noteosuchus* (Fig. 6A).

The calcaneum has been modified from the primitive platelike condition by the development of a laterally extending tuber. The distal edge is thin, and a thickened medial buttress extends transversely across the bone to the expanded cartilage-covered lateral edge. Judging from Young's illustration of the calcaneum of *Chasmatosaurus yuani,* the proximal edge was covered by unfinished bone, as it is in the early rhynchosaur *Noteosuchus* (Fig. 6A).

The centrale has shifted its position so that it is now located laterally, rather than distally, to the astragalus. It may aid in support of the tibia.

Cruickshank (1972), based on the similarity of the tarsus of *Chasmatosaurus* and early rhynchosaurs and the presence in both of a downturned premaxilla, suggested that *Chasmatosaurus* was a carnivorous rhynchocephalian. If the proterosuchian tarsus was restricted to these animals, it would suggest that *Chasmatosaurus* is phylogenetically a rhynchosaur and thus would bring into question the validity of using the proterosuchian tarsus as the primitive archosaur pattern. However, a number of additional groups of diapsid reptiles have a tarsus that, in so far as comparison is possible, is like that of *Chasmatosaurus.* The tarsus of *Prolacerta* (Gow, 1975, Fig. 33) shows all the advanced features seen in *Chasmatosaurus* and early rhynchosaurs. As would be expected, the aquatic members of the Prolacertiformes show a decrease in the ossification of the tarsus. Despite this, mature specimens of *Tanystropheus* (Wild, 1973; Fig. 75) and *Macrocnemus* (Peyer, 1937; Pl. 56, Fig. 2) show the diagnostic features of a laterally directed dorsoventrally compressed tuber on the calcaneum, and a complex concave-convex articulation between the astragalus and calcaneum. A proterosuchian tarsus is also seen in *Protorosaurus* from the Permian of Europe (von Meyer, 1856, Pl. 9), and *Trilophosaurus* from the Triassic of Texas (Fig. 4).

At first glance, this assemblage of reptiles seems to be an unnatural one, bringing together animals with markedly different adaptations and skull configurations. However, a more detailed consideration shows that this assemblage is not as artificial as first
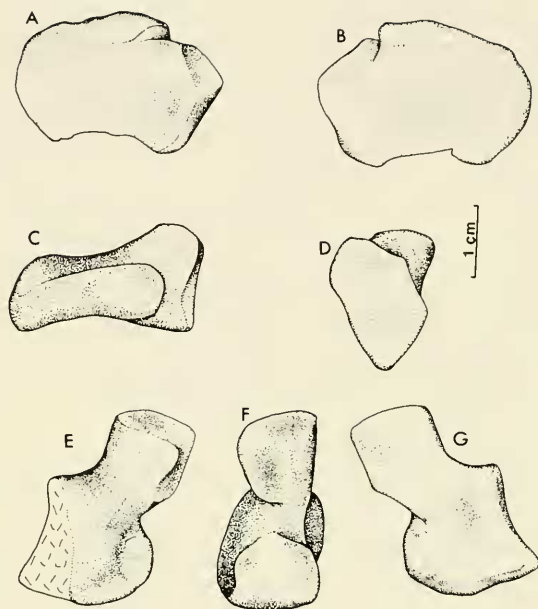
Figure 4.   The right astragalus and calcaneum of *Trilophosaurus*. Calcaneum in A) ventral, B) dorsal, C) proximal, and D) distal views; astragalus in E) ventral, F), medial, and G) dorsal views. Calcaneum: specimen TMM 31025-258; astragalus: specimen TMM 31025-259, Texas Memorial Museum.

appears. *Prolacerta* and *Protorosaurus* have long been recognized as being closely related (Camp, 1945; Watson, 1958). Romer (1956) denied the presence of such a relationship, choosing to place *Protorosaurus* in the Euryapsida because of the presumed presence of a solid cheek. However, as noted by Chatterjee (1980), much uncertainty about the structure of the skull of *Protorosaurus* exists. Details of the skull and postcranial skeleton that are known for certain are similar to *Prolacerta*, and Chatterjee unites these genera in the suborder Prolacertiformes. Gow (1975) concluded on the basis of evidence from the skull of *Prolacerta* that the Prolacertiformes are related to archosaurs.

The remaining groups in this assemblage, rhynchosaurids and trilophosaurids, have highly specialized skulls that could be derived from any primitive diapsid, so the skull neither supports nor negates a relationship between these groups and the archosaur-protoro-

saurid-prolacertid group. Postcranially, both trilophosaurids and rhynchosaurids are less specialized, and a similarity in the structure of their postcranial skeletons and the postcranial skeleton of some members of the archosaur-protorosaurid-prolacertid group has been noted (Gregory, 1945; Carroll, 1976), although it is not certain whether these represent derived features or primitive features widespread in diapsid reptiles.

Thus, there seems to be no need to hypothesize a multiple origin of the proterosuchian tarsus. If rhynchosaurs, prolacertiformes, prolacertids, trilophosaurids, and archosaurs are a natural group, the proterosuchian tarsus could have originated only once. One implication of this is that the proterosuchian tarsus is the primitive archosaur tarsus and is the ultimate structural ancestor of the various kinds of tarsi seen in advanced archosaurs. In some cases, an intermediate structural complex may have been present, but, as shown by Cruickshank (1979), the proterosuchian tarsus was probably the direct structural antecedent of the crocodile-normal tarsus. It is useful to identify the structural changes that would have occurred during this transition before considering the structure and origin of the crocodile-reversed tarsus.

ORIGIN OF THE CROCODILE-NORMAL TARSUS

As recognized by Cruickshank (1979), the astragalus-centrale unit of the proterosuchian tarsus is directly comparable to the astragalus of the crocodile-normal tarsus (Fig. 5). The area distal to the perforating foramen is homologous to the cone-shaped articular surface of the crocodile-normal tarsus, but differs in being smaller and less strongly curved. The area proximal to the perforating foramen is homologous to the dorsal half of the notch on the lateral edge of the crocodile-normal astragalus, the main difference being that in the proterosuchian tarsus this surface is separated from the distal surface by finished bone.

The calcaneum of the crocodile-normal and proterosuchian tarsi (Fig. 6) differs in the orientation of the calcaneal tuber; in the proterosuchian tarsus, this is directed laterally, while in the crocodile-normal tarsus, this is directed more posteriorly. If the calcaneal tuber of the proterosuchian tarsus were oriented so that it extended posteriorly, the articular surface for the fibula and astragalus would be oriented along the long axis of the bone rather
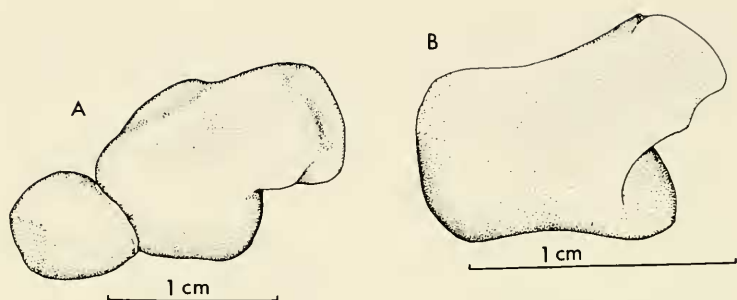
Figure 5. The left astragalus of the proterosuchian and crocodile-normal tarsus in anterior view. A) astragalus and centrale of *Noteosuchus;* B) astragalus of *Gracilisuchus.* Not drawn to scale. *Noteosuchus* based on cast of Albany Museum 3591. *Grasilisuchus* based on cast of specimen in collection of Paleontologia Vertebrados de la Fundacion M. Lillo.
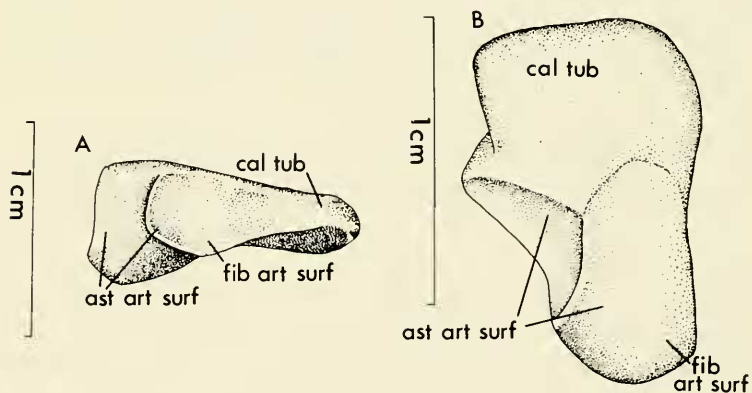

Figure 6. The left calcaneum of the proterosuchian and crocodile-normal tarsus. A) calcaneum of *Noteosuchus;* B) calcaneum of *Gracilisuchus.*

Abbreviations: ast art surf, astragalar articular surface; cal tub, calcaneal tuber; fib art surf, fibular articular surface.

than across it. A simple enlargement of the articular surface, together with the extension of the proximal portion of the astragalar articular surface onto the medial edge of the perforating foramen, would form the wheel-shaped articular surface of the crocodile-normal calcaneum. An enlargement of the ventral half of the articular surface for the astragalus would form the medial flange of the crocodile-normal calcaneum.

Thus structurally, the proterosuchian tarsus is an excellent ancestor of the crocodile-normal tarsus. The mechanical changes involved in this transition were probably minor, since, as noted by Thulborn (1980), the joint between the astragalus and calcaneum was probably movable in the proterosuchian tarsus.

THE CROCODILE-REVERSED TARSUS

The crocodile-reversed tarsus is best known in the ornithosuchid *Riojasuchus* (Bonaparte, 1971, 1975b). Dorsally, the calcaneum (Fig. 7B) has an articular surface that is convex both mediolaterally and proximodistally. This surface supports the fibula along its lateral edge and the astragalus along its medial edge. These are exactly the relationships of the wheel-shaped articular surface of the crocodile-normal tarsus (Fig. 8A-B). The major difference is that the medial edge of this area is hypertrophied in *Riojasuchus* to form a medially directed process. This process is functionally equivalent to the ventral flange of the crocodile-normal calcaneum in that it underlies the astragalus (Fig. 8C-D). Consequently, it is not surprising that the ventral flange or an homologous area is not present in the crocodile-reversed calcaneum. The absence of the ventral flange is associated with a reduction in the width of the calcaneal tuber; in the crocodile-reversed tarsus, the calcaneal tuber does not extend the full width of the bone. In addition, the tuber of the crocodile-reversed tarsus is distinctive in that its distal end curves medially and is without a groove for the tendon of the gastrocnemial muscles.

The differences in structure of the astragalus of the crocodile-normal and crocodile-reversed tarsus correspond to the differences in structure of the calcaneum: the hypertrophy of the medial edge of the wheel-shaped articular surface is associated with the elongation of the overlying portion of the astragalus, and the loss of the ventral flange is associated with the loss of the cone-shaped articular surface.
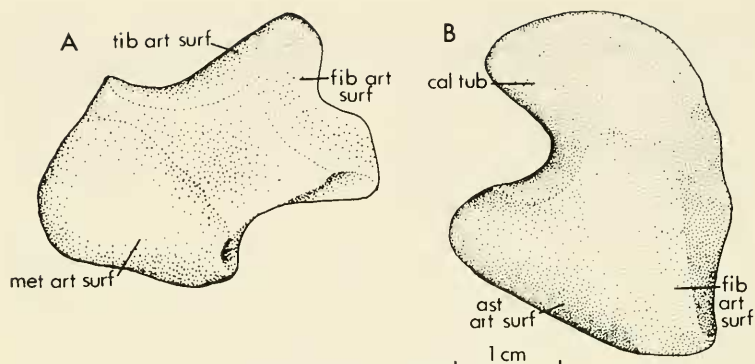
Figure 7.   The left astragalus and calcaneum of the crocodile-reversed tarsus. A) Astragalus and B) calcaneum of *Riojasuchus.* Drawn from cast of PVL 3827, Paleontologia Vertebrados de la Fundacion M. Lillo.

Abbreviations: ast art surf, astragalar articular surface;   cal tub, calcaneal tuber;   fib art surf, fibular articular surface;   met art surf, metatarsal articular surface;   tib art surf, tibial articular surface.

From this comparison, it can be seen that the crocodile-normal tarsus is a plausible ancestor of the crocodile-reversed tarsus. The major changes involved in such a transition would be the medial elongation of the wheel-shaped articular surface of the calcaneum and the loss of the ventral flange. Derivation of the crocodile-reversed tarsus directly from the primitive archosaur tarsus is also possible. However, derivation of the crocodile-normal tarsus from the crocodile-reversed tarsus can be discounted as being improbable since it would involve the redevelopment of the ventral flange, a structure that is present in the crocodile-normal tarsus and the primitive archosaur tarsus but absent in the crocodile-reversed tarsus.

Given this relationship of the crocodile-normal and crocodile-reversed tarsi, the structure of the tarsus cannot be used to exclude *Gracilisuchus* from the Ornithosuchidae. Rather, the systematic position of *Gracilisuchus* has implications for the evolution of the tarsus. If *Gracilisuchus* is a true ornithosuchid, the crocodile-normal tarsus must have given rise to the crocodile-reversed tarsus, and the structure of the tarsus has little real phylogenetic significance. If however, *Gracilisuchus* is not an ornithosuchid, the crocodile-reversed tarsus may have originated independently from
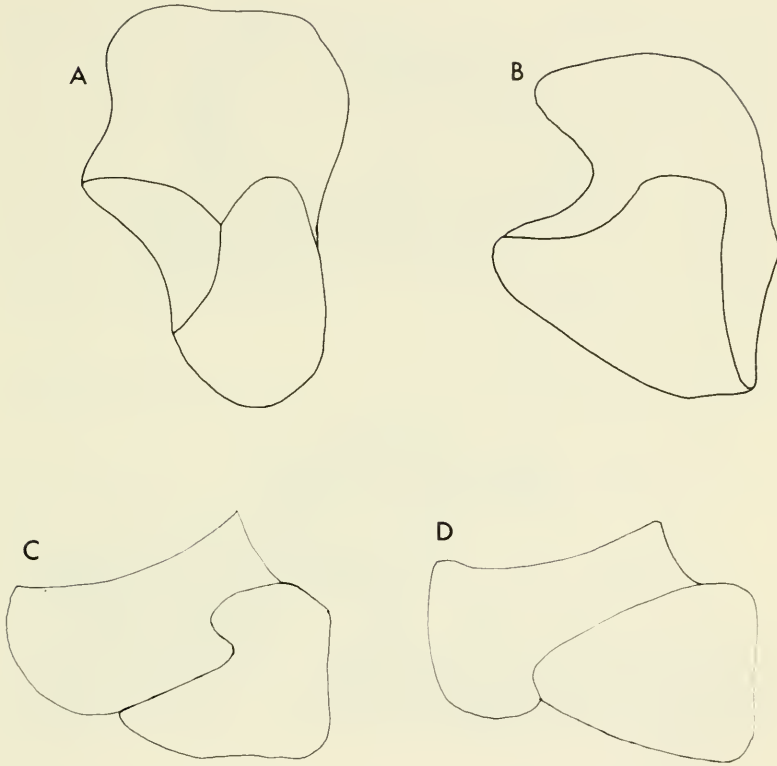
Figure 8. The left calcaneum of the crocodile-normal and crocodile-reversed tarsi. A) crocodile-normal calcaneum of *Gracilisuchus* in proximal view; B) crocodile-reversed calcaneum of *Riojasuchus* in proximal view; C) section through an articulated crocodile-normal astragalus and calcaneum; D) section through an articulated crocodile-reversed astragalus and calcaneum. Not drawn to scale.

the proterosuchian tarsus, and the presence of the crocodile-reversed tarsus can be used as the defining feature of some taxonomic group. Thus it is necessary to reconsider the relationships of *Gracilisuchus*.

THE RELATIONSHIPS OF *GRACILISUCHUS*

The skull of *Gracilisuchus* was reconstructed by Romer (1972) on the basis of MCZ 4117, a complete, three dimensional skull. One of

the unusual features seen in this skull is a small lower temporal opening. However, other material, particularly MCZ 4116 and MCZ 4118, show that MCZ 4117 has been slightly crushed and the quadratojugal and squamosal have been displaced. In MCZ 4116, the preorbital bar is slender and the antorbital opening is larger than in MCZ 4117 (Fig. 9A). In MCZ 4118, the postorbital bar is tall and slender, the quadratojugal and squamosal are separated from the postorbital, and the lower temporal opening is large and rectangular (Fig 9B). Based on these skulls, the arrangement of the temporal region and the height of the face in the reconstruction of the skull of *Gracilisuchus* is modified (Fig. 9B).

Gracilisuchus differs from the advanced ornithosuchids as defined by Bonaparte (1975b) (Fig. 10) in the following features:

1) The antorbital fenestra is rectangular in *Gracilisuchus* and is triangular in the advanced ornithosuchids.

2) The ventral border of the orbit is round in *Gracilisuchus,* and a distinct antorbital ramus of the jugal is not present. In the advanced ornithosuchids, a distinct preorbital ramus of the jugal is present; this is close to the postorbital ramus at its base, so the ventral margin of the orbit is pointed.

3) The quadratojugal of *Gracilisuchus* is a tall, slender element that extends nearly the full height of the lower temporal opening. In the advanced ornithosuchids, the quadratojugal is broader and is limted to the ventral half of the lower temporal opening.

4) The upper tooth row is complete, and all the teeth of the lower jaw fit inside the upper teeth row in *Gracilisuchus.* In advanced ornithosuchids, a gap is present between the anterior tooth of the maxilla and the posterior tooth of the premaxilla, with the anterior one or two dentary teeth passing lateral to the maxilla in this gap.

5) In *Gracilisuchus,* the lower temporal fenestra is rectangular, and no anterior inflection of the quadratojugal and squamosal is present. In the advanced ornithosuchids, a large anterior inflection of the quadratojugal and squamosal results in the presence of an L-shaped lower temporal fenestra.

6) In *Gracilisuchus,* the squamosal has a peculiar, posteriorly concave flange on its dorsal end. No such flange is present in the advanced ornithosuchids.
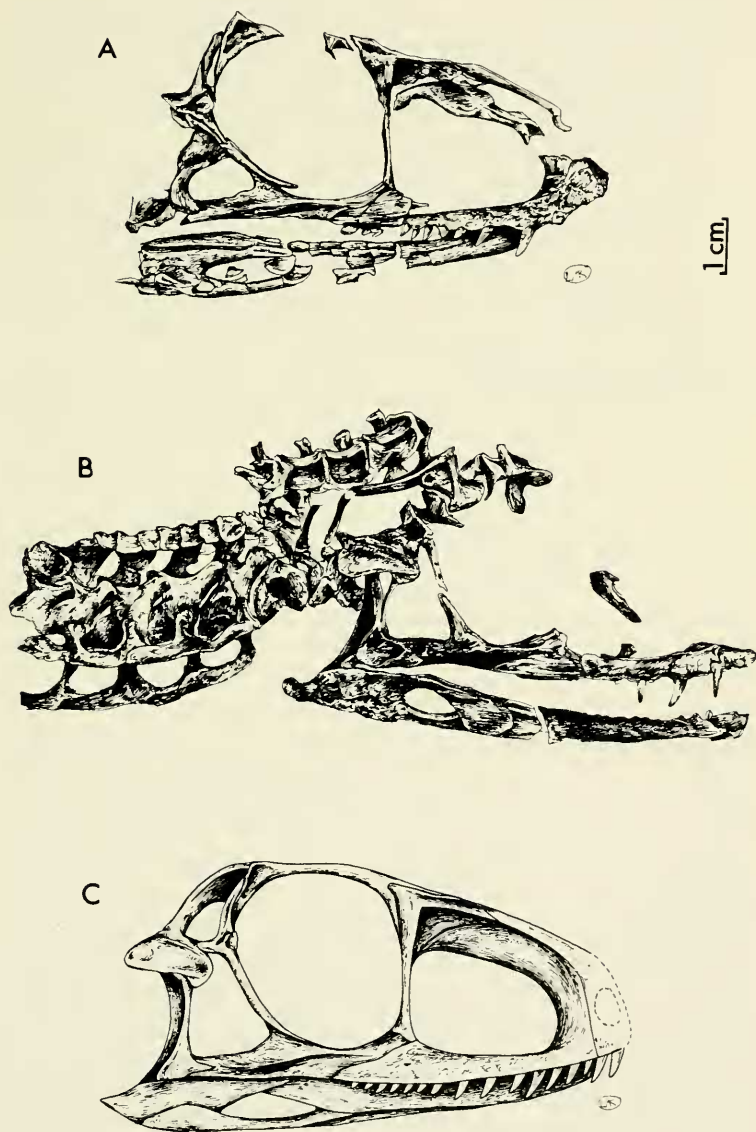
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Figure 9. The skull of *Gracilisuchus*. A) specimen drawing of MCZ 4116; B) specimen drawing of MCZ 4118; C) reconstruction of skull.

7) In *Gracilisuchus,* the posterior end of the dentary extends dorsal to the mandibular fenestra. In the advanced ornithosuchids, the posterior end of the dentary is forked, with one branch extending dorsal and one branch extending ventral to the lateral mandibular fenestra.

8) In *Gracilisuchus,* the splenial forms the ventral margin of the jaw along the posterior half of the dentary. In the advanced ornithosuchids, the splenial is restricted to the inner surface of the jaw.

9) In *Gracilisuchus,* the cervical vertebrae are not keeled. In the advanced ornithosuchids, the cervical vertebrae, where known (*Riojasuchus* and *Ornithosuchus*), are keeled.

10) In *Gracilisuchus,* there are two pairs of dermal scutes per vertebra in the cervical region of the vertebral column. In the advanced ornithosuchids, where known (*Ornithosuchus* and *Riojasuchus*), there is one pair of scutes per vertebra.

This list of differences between *Gracilisuchus* and the advanced ornithosuchids shows that the advanced ornithosuchids are more similar to each other than to *Gracilisuchus.* But these features by themselves do not demonstrate that *Gracilisuchus* is not an ornithosuchid; *Gracilisuchus* occurs much earlier in time than the advanced ornithosuchids, so the differences may represent successive grades of evolution in a single radiation. In order to be used phylogenetically, it is necessary to determine which of the character-states represent derived features. *Euparkeria* (Fig. 10D), the oldest known pseudosuchian, had traditionally been considered to be the structural ancestor of later pseudosuchians and thus can be used as the outgroup in determining which character-states are primitive or advanced.

Features that are shared by *Gracilisuchus* and *Euparkeria*, and thus can be considered primitive, are the presence of a complete upper tooth row with all the dentary teeth fitting inside the upper tooth row, the shape of the lower temporal fenestra, and the shape of the antorbital fenestra (features 1, 4, and 5 in the above list). In all other features, *Euparkeria* is like the advanced ornithosuchids and unlike *Gracilisuchus:* the jugal has a well-developed antorbital process, and the base of this is near the postorbital process; the squamosal is without the peculiar posteriorly concave flange seen in *Gracilisuchus*; the posterior end of the dentary is forked, with a branch above and a branch below the lateral mandibular fenestra;
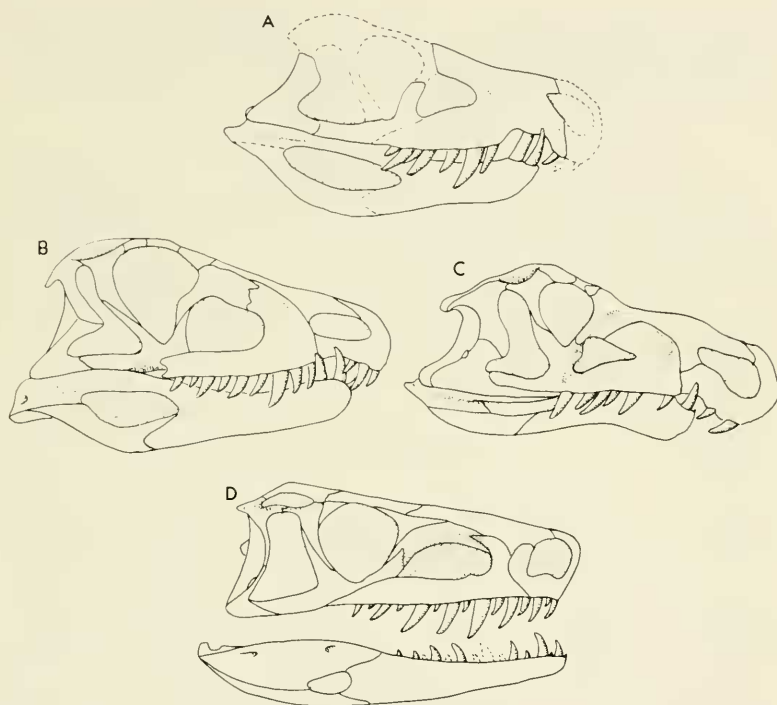
Figure 10.   The skulls of the advanced ornithosuchids and *Euparkeria.* A) *Venaticosuchus;* B) *Ornithosuchus;* C) *Riojasuchus;* D) *Euparkeria.* From Bonaparte, 1975.

the splenial is restricted to the internal surface of the lower jaw; the cervical vertebrae are keeled; and one pair of dermal scutes is present per vertebral segment. For these features, the character-state present in the advanced ornithosuchids must be considered primitive, and the *Gracilisuchus* condition derived.

Thus, if an ornithosuchid, *Gracilisuchus* is derived from the ornithosuchid pattern in a way different from the advanced ornithosuchids. Alternatively, *Gracilisuchus* may be a member of a radiation distinct from that of ornithosuchids. This latter possibility is suggested by the presence of some of the derived features of *Gracilisuchus* in *Sphenosuchus, Pseudohesperosuchus,* and *Lewisuchus,* pseudosuchians that are thought to be unrelated to ornithosuchids (Romer, 1972). These features include the tall,

slender quadratojugal, the posterior flange on the squamosal (known in *Pseudohesperosuchus* and *Sphenosuchus*), and the presence of unkeeled cervical vertebrae (known in *Lewisuchus*).

THE TARSUS OF *EUPARKERIA*

The similarity between ornithosuchids and *Euparkeria* raises the possibility that *Euparkeria* is closely related to the Ornithosuchidae, rather than being a generalized primitive pseudosuchian. Such a relationship is supported by the structure of the tarsus. The astragalus and calcaneum of *Euparkeria* were illustrated by Bonaparte (1975) and Cruickshank (1979). As noted by these authors, these elements are directly comparable to those of the crocodile-reversed tarsus (Fig. 11). The dorsal portion of the articular surface of the calcaneum is divisible into two areas, a narrow area along the lateral edge of the bone that would have articulated with the fibula, and a medial area that would have articulated with the astragalus. The astragalar area is in the shape of a portion of a cone with its apex directed medially. No area comparable to the ventral flange of the crocodile-normal tarsus is present. The calcaneal tuber is directed posteriorly and is narrow.

Thus the calcaneum of *Euparkeria* is similar to the crocodile-reversed tarsus in all the features by which the crocodile-normal and crocodile-reversed tarsi differ. Of special importance is the absence of an area homologous to the ventral flange of the astragalus of the crocodile-normal tarsus. As was argued above, the absence of this area prevents derivation of a crocodile-normal tarsus from a crocodile-reversed tarsus without the redevelopment of a lost structure. On this basis, *Euparkeria* can be considered to be more closely related to the ornithosuchids than to any pseudosuchian with a crocodile-normal tarsus.

THE TARSUS OF *ERYTHROSUCHUS*

An additional problem to be considered is the relationship of *Erythrosuchus*. Sill (1974) showed that a striking similarity exists between the skull of *Erythrosuchus* and rauisuchids, so that a relationship between these two groups is probable. Cruickshank (1978, 1979), however, felt that the tarsus of *Erythrosuchus* was most similar to that of Euparkeria, and placed *Erythrosuchus* with *Euparkeria* and the ornithosuchids in his Ornithosuchoidea.
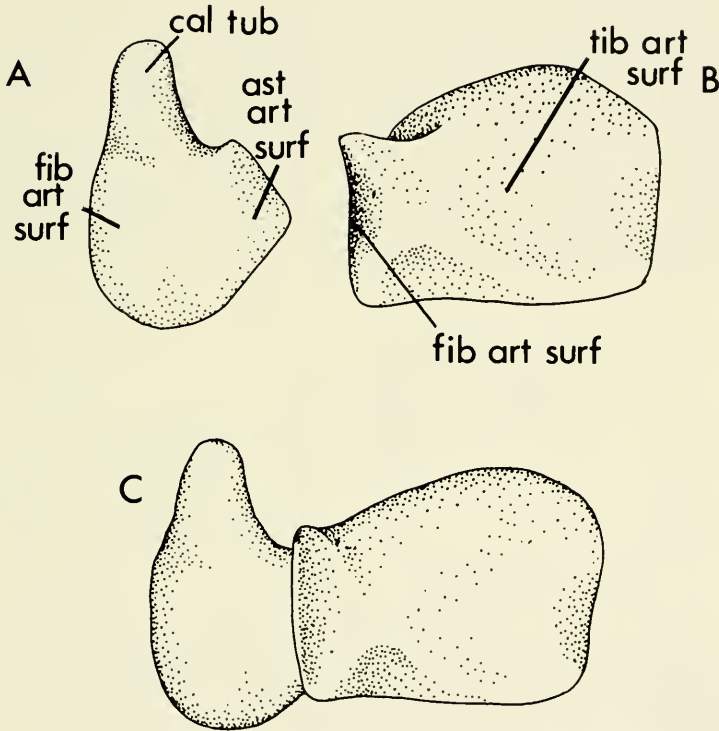
Figure 11.   The right astragalus and calcaneum of *Euparkeria*. A) astragalus; B) calcaneum; and C) astragalus and calcaneum in articulation. A and B from Bonaparte (1975), C based on drawings of South African Museum specimen SAM 6049 made by J. Bonaparte.

Abbreviations: ast art surf, astragalar articular surface;   cal tub, calcaneal tuber;   fib art surf, fibular articular surface;   tib art surf, tibial articular surface.

A general similarity between the tarsus of *Erythrosuchus* and *Euparkeria* is present, but this can be attributed to the poor ossification of the bones. More fundamental is the similarity between the tarsus of *Erythrosuchus* and *Chasmatosaurus*. A comparison of the calcaneum of these two animals (Fig. 12) shows that the calcaneal tuber extends laterally, has thin proximal and distal edges, and has a thickened medial buttress that extends across the tuber to an expanded cartilage-covered lateral edge. The poor ossification of the astragalus of *Erythrosuchus* obscured the structure of the articulation between the astragalus and calcaneum,
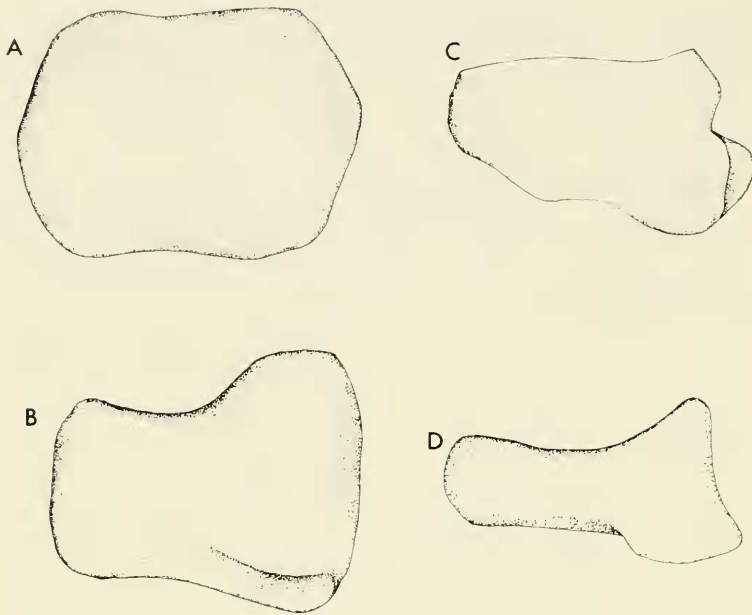
Figure 12.   The left calcaneum of *Erythrosuchus* in A) ventral, and B) distal views; and *Chasmatosaurus* in C) ventral, and D) distal views. *Erythrosuchus* drawing based on cast of Bernard Price Institute F. 2069 M 405, *Chasmatosaurus* drawing based on cast of NM C 3016, Nasionale Museum, Bloemfontein.

although Cruickshank (1978) identifies a perforating foramen, a primitive feature that is also present in *Chasmatosaurus*.

Thus the tarsus of *Erythrosuchus* is best considered a poorly ossified proterosuchian tarsus. A reduction of ossification is commonly seen in aquatic animals, and probably reflects an adaptation for an aquatic habitat, rather than the development of a mechanically distinct structural complex. A fully terrestrial erythrosuchid would, therefore, be expected to have a tarsus like that of *Chasmatosaurus*. Since this kind of tarsus is the structural ancestor of the crocodile-normal tarsus, the structure of the erythrosuchid tarsus neither supports nor negates a relationship between erythrosuchids and rauisuchids. If a relationship between erythrosuchids and rauisuchids is accepted on the basis of similarities in the skull, it is necessary to assume that the crocodile-normal tarsus originated after the origin of this radiation of thecodonts, and therefore the tarsus cannot be used as the defining feature of the group.

SUMMARY

A summary of the relationships suggested above may be made in the form of a phylogenetic diagram (Fig. 13). According to this phylogeny, many of the higher taxa of diapsid reptiles are artificial assemblages, and major modifications of reptilian classification are necessary to accurately reflect reptilian relationships. It would, however, be useful to test these relationships through examination of other structural complexes before making the necessary changes.

Figure 13. The interrelationships of thecodonts.

ACKNOWLEDGMENTS

LITERATURE CITED

BONAPARTE, J. F. 1971. Los tetrapodos del sector superior de la formation Los Colorados, La Rioja, Argentina. Opera Lilloana, **22:** 1–183.

———. 1975a. Nuevos materials de *Lagosuchus talampayensis* Romer (Thecodontia-Pseudosuchia) y su significade en el origen de los Saurischia. Acta Geol. Lilloana, **13:** 5–87.

———. 1975b. The family Ornithosuchidae (Archosauria: Thecodontia). Colloques int. Cent. Natn. Rech. Scient. No. 218, pp. 485–506.

CAMP, C. L. 1945. *Prolacerta* and the protorosaurian reptiles. Am. J. Sci., **243:** 17–32, 84–101.

CARROLL, R. L. 1976. *Noteosuchus,* the oldest known rhynchosaur. Ann. S. Afr. Mus., **72:** 37–57.

CHARIG, A. J., AND H. -D. SUES. 1976. Proterosuchia, pp. 11–39. *In* A. J. Charig, B. Krebs, H. -D. Sues, and F. Westphal, Handbuch der Palaoherpetologie, 13, Stuttgart and Portland, Gustav Fischer, 137 pp.

CHATTERJEE, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper-Triassic Maleri Formation of India. Paleontology, **21:** 83–127.

———. 1980. Malerisaurus, a new eosuchian reptile from the late Triassic of India. Phil. Trans. Roy. Soc. Lond. (B). **291:** 163–200.

CRUICKSHANK, A. R. I. 1972. The proterosuchian thecodonts, 89–119. *In* K. A. Joysey, and T. S. Kemp (eds.), Studies in Vertebrate Evolution: Essays Presented to Dr. F. R. Parrington F. R. S. Edinburgh, Oliver and Boyd, 284 pp.

———. 1978. The pes of *Erythrosuchus africanus* Broom. J. Linnean Soc. (Zool.), **62:** 161–178.

———. 1979. The ankle joint in some early archosaurs. S. Afr. J. Sci., **75:** 168–178.

GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Paleontol. Afr., **18:** 89–131.

GREGORY, J. T. 1945. Osteology and relationships of *Trilophosaurus.* U. of Texas Publ. No. 4401, pp. 273–359.

KREBS, B. 1963. Bau und Function des Tarsus eines Pseudosuchiers aus der Trias des Monte San Giorgio (Kanton Tessin, Schweiz.). Paläontol. Z., **37:** 88–95.

———. 1965. *Tictinosuchus ferox* nov. gen., nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giogio. Schweiz. Paläontol. Abh., **81:** 1–140.

———. 1973. Der Tarsus von *Rauisuchus* (Pseudosuchia, Mittel Trias). Mitt. Bayer. Staatsamml. Paläontol. Hist. Geol., **13:** 95–101.

PEYER, B. 1937. Die Triasfauna der Tessiner Kalkalpen, XII *Macrocnemus bassanii* Nopsca. Schweiz. Paläontol. Abh., **59:** 1–140.

ROMER, A. S.   1956.   The Osteology of the Reptiles. Chicago, University of Chicago Press, 772 pp.

———.   1971.   The Chañares (Argentina) Triassic reptile Fauna X. Two new but incompletely known long-limbed pseudosuchians. Mus. Comp. Zool., Breviora No. 378, pp. 1–10.

———.   1972.   The Chañares (Argentina Triassic Reptile Fauna, XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipaniaicorum,* gen. et sp. nov. Mus. Comp. Zool., Breviora No. 389, pp. 1–24.

SAWIN, H. J.   1947.   The pseudosuchian reptile *Typothorax meadei.* J. Paleontol., **21:** 201–238.

SILL, W. D.   1974.   The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. Bull. Mus. Comp. Zool., **146:** 317–362.

THULBORN, R. A.   1980.   The ankle joints of archosaurs. Alcheringa, **4:** 241–261.

VON MEYER, H.   1856.   Zur Fauna der Vorwelt, Saurier aus dem Kupferschiefer der Zechstein-Formation. Frankfut-am-main.

WALKER, A. D.   1961.   Triassic reptiles from the Elgin area: *Stagonolepis, Dasygnathus* and their allies. Phil. Trans. Roy. Soc. Lond. (B), **244:** 103–204.

———.   1970.   A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. Phil. Trans. Roy. Soc. Lond. (B), **257:** 323–372.

WATSON, D. M. S.   1958.   On *Millerosaurus* and the early history of the sauropsid reptiles. Phil. Trans. Roy. Soc. Lond. (B), **240:** 355–400.

WILD, R.   1973.   Die Triasfauna der Tessiner Kalkalpen XXIII. Tanystropheus longobardicus (Bassani) (Neue Ergebnisse). Schweiz. Paläontol. Abh., **95:** , 1–162.

YOUNG, C. C.   1936.   On a new *Chasmatosaurus* from Sinckiang. Bull. Geol. Soc. China, **15:** 291–320.

———.   1964.   The pseudosuchians in China. Palaeontol. Sinica, New Ser. C, **19:** 1–205.